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Butterfly migration: are synoptic-scale wind systems important?

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ABSTRACT. 1. If synoptic-scale wind systems are important in determining long-distance movements of butterflies, a portion of the variation in daily counts of migrants at a site should be explainable by prior winds.

2. Using special flight traps near Gainesville, Florida, U.S.A., from 29 August until 12 November 1978, we made replicated, continuous counts of four migrant species: *Phoebis sennae*, *Urbanus proteus*, *Agraulis vanillae* and *Precis coenia.*

3. Significant SSE-ward flights occurred for one or more of the four species on 47 days between 5 September and 6 November (Fig. 1).

4. Seasonal changes in numbers of migrants were similar for the four species (Fig. 1). Median fall migrants were trapped between 22 September (*A.vanillae*) and 1 October (*U.proteus* and *P.sennae*).

5. Daily fluctuations in total numbers of migrants were largely attributable to local weather, viz temperature, wind speed and cloud cover (Fig. 2).

6. Neither local wind direction (Fig. 3) nor back-tracking the positions of air parcels (Fig. 4) helped explain the daily fluctuations.

7. The characteristic autumn weather patterns of south-eastern U.S.A. and the day-to-day steadiness of the numbers of migrants are incompatible with the hypothesis that synoptic-scale wind systems are important in determining butterfly migrations through Gainesville, Florida, in the autumn.

Introduction

Butterflies are well known as insect migrants because many species make conspicuous unidirectional flights close to the ground with all, or nearly all, individuals maintaining the same general compass direction (Williams, 1930, 1958). The flights continue in the same direction in spite of major obstacles, time of day, or shifts in wind direction. Flights through an area may last for days or weeks and occur at the same season or seasons each year. Their time of occurrence, direction and geographical distribution often fit the assumption that migrating individuals are flying hundreds of kilometres to more favourable habitats. For example, each autumn over much of eastern United States numerous monarch butterflies (*Danaus plexippus*) are observed flying southward or south-westward; in the spring smaller numbers are sometimes noted flying northward. Since monarchs are known to overwinter no farther north than the Gulf States, Williams (1930) and others postulated that individuals made long-distance autumn flights to overwintering areas and similar spring flights in the reverse direction to northern breeding areas. F. A. & N. R. Urquhart (1960, 1978, 1979) confirmed this hypothesis by a tagging programme: individuals tagged in

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Ontario and the northern states in late summer were recaptured in Florida, Texas and Mexico at distances as great as 3000 km from the point of release; individuals tagged in Mexico in the winter were recaptured as far as 2000 km to the north or north-east in the spring.

Butterflies seen migrating are generally in the *boundary layer* – the layer near the ground in which air movement is less than their air speed, enabling them to maintain control of their tracks (Johnson, 1969, p. 132). Because of such observations, Williams (1930, 1958), and others (e.g. Baker, 1971, 1978), have concluded that migrating butterflies determine their direction of travel directly and do not rely on wind as a major means of transport. However, Johnson (1969, 1971) advanced a counter-hypothesis: since individual butterflies are watched only for short distances and since there are numerous records of butterflies flying well above the boundary layer, their major transport may be in the upper air. The near-ground movements may be of minor consequence and misleading – as in the case of migratory locusts – and the principal direction and tactics of displacement may depend on synoptic-scale weather systems. Johnson concluded (1969, p. 540), that 'the controversy that now exists about this subject cannot yet be settled, for the necessary data do not exist.'

We monitored four species of butterflies that annually migrate through north peninsular Florida to generate data that might settle the controversy. *Phoebis sennae* (Linnaeus), *Urbanus proteus* (Linnaeus), *Agraulis vanillae* (Linnaeus), and *Precis coenia* (Hubner) are conspicuous SSE-ward migrants each fall (Arbogast, 1966; Balciunas & Knopf, 1977; Edwards & Richman, 1977). The four species reproduce in the northern states each summer but apparently overwinter only in the South. The autumn flights seem to be from soon-to-be-lethal summer breeding grounds to areas permitting survival and, in some instances, breeding during the winter. Walker (1978, 1980) tested two-way linear flight traps as a means of continuously monitoring flights within 2 m of the ground. Each trap had two 6 × 2 m openings, and when the traps were set perpendicular to the axis of the Florida peninsula, butterflies flying SSE ±90° were trapped separately from those flying NNW ±90°. Estimated numbers of migrants crossing each metre of an imaginary ENE–WSW line during autumn ranged from 10 (*P.coenia*, autumn 1978) to 4000 (*U.proteus*, autumn 1975).

We reasoned that daily changes in numbers of near-the-ground migrants provide a test of whether their source is previous transport by upper air or migrant-directed flight in the boundary layer. If the numbers of migrants fluctuate in accord with the permissiveness of local and 'upstream' boundary-layer weather and are independent of previous wind direction, then no transport by upper air is evidenced. If numbers of migrants fluctuate in accord with the arrival of synoptic-scale weather systems having favourable configurations for passive transport of butterflies from source areas to where they will fly low and be counted, then transport in upper air is indicated.

Methods

During autumn 1978 boundary-layer migration of butterflies was continuously sampled with four, 5.9 m, two-way flight traps (Walker, 1980) 10 km west of Gainesville (Sec. 27, R18E, T9S). The traps were set in a WSW–ENE line 7.4 m apart near the centre of a ploughed and disced field and tended daily from 29 August until 12 November. The catching devices on as many as three of the traps malfunctioned during the first 12 days; fully replicated counts began on 10 September.

Results

Of 2868 specimens captured of the four species, 2721 (95%) were flying SSE-ward ±90° (Fig. 1). The seasonal patterns of migration for the four were similar. The capture date of the median autumn migrant ranged from 22 September for *A.vanillae* to 1 October for *P.sennae* and *U.proteus*. Daily fluctuations in numbers were generally synchronous; for example, counts for all species were unusually low for 29 and 30 September and unusually high for 5 October.

Daily fluctuations in total numbers of migrants were examined for dependence on weather conditions in the boundary layer, represented by the surface weather reported

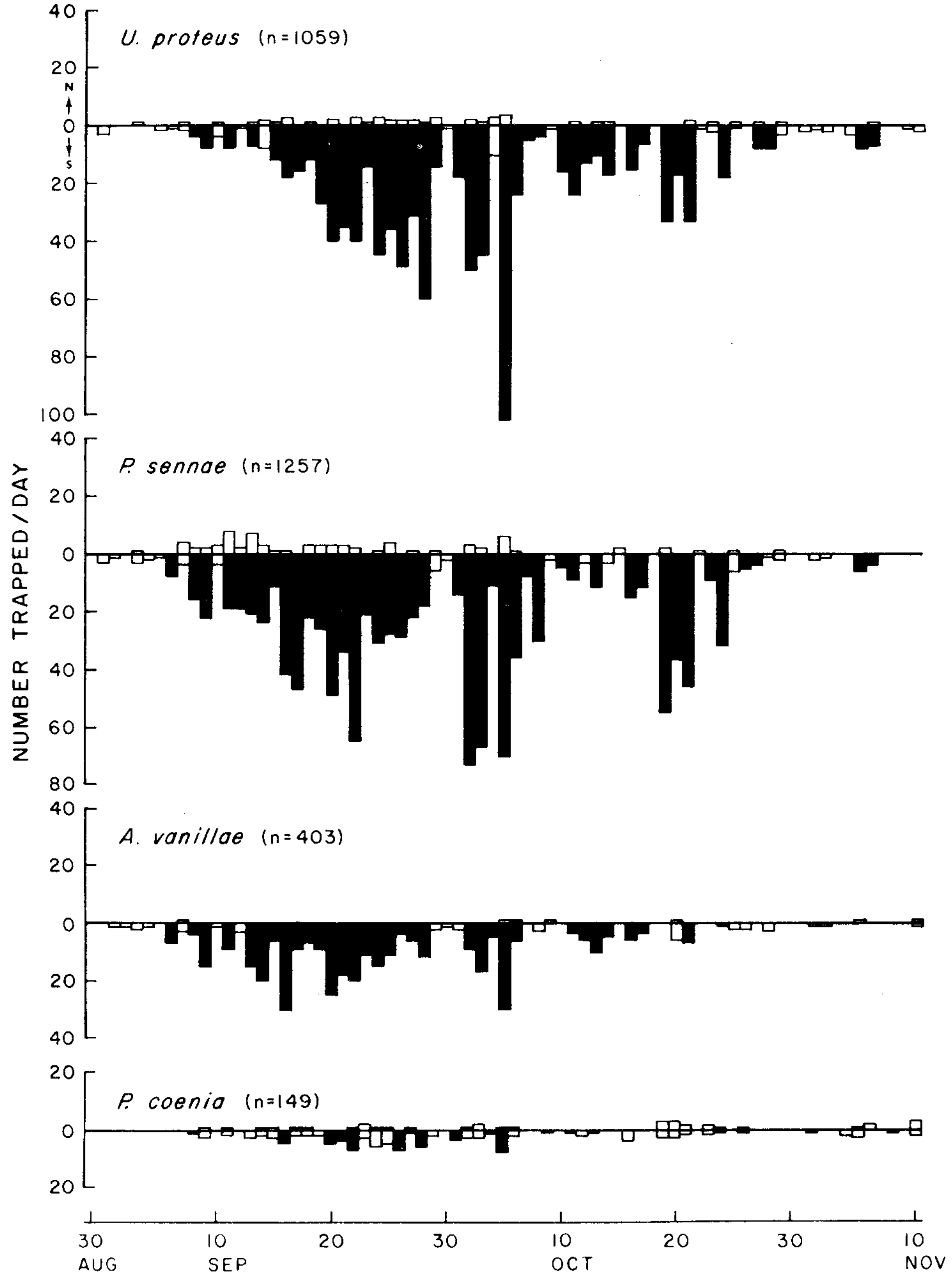

FIG. 1. Daily catches of four species of butterflies during autumn migration, 1978, Gainesville, Florida, in four two-way, 5.9 m, linear Malaise traps set perpendicular to the axis of the Florida peninsula. Individuals intercepted flying SSE-ward ±90° are denoted by downward bars; those flying NNW-ward ±90° by upward bars. Solid bars indicate a significant bias ($P < 0.05$) in the day's catch in that direction (always SSE-ward).

at Gainesville (NOAA, 1978a). Daily weather was scored 0–8 on the basis of the number of hourly weather readings during 09.00–16.00 hours LST meeting four criteria of suitability, namely wind $< 4.6\ \mathrm{m\,s^{-1}}$, temperature $> 21^{\circ}\mathrm{C}$, total sky cover $< 95\%$ and opaque sky cover $< 80\%$. The relation between weather and intensity of migration is depicted in Fig. 2.

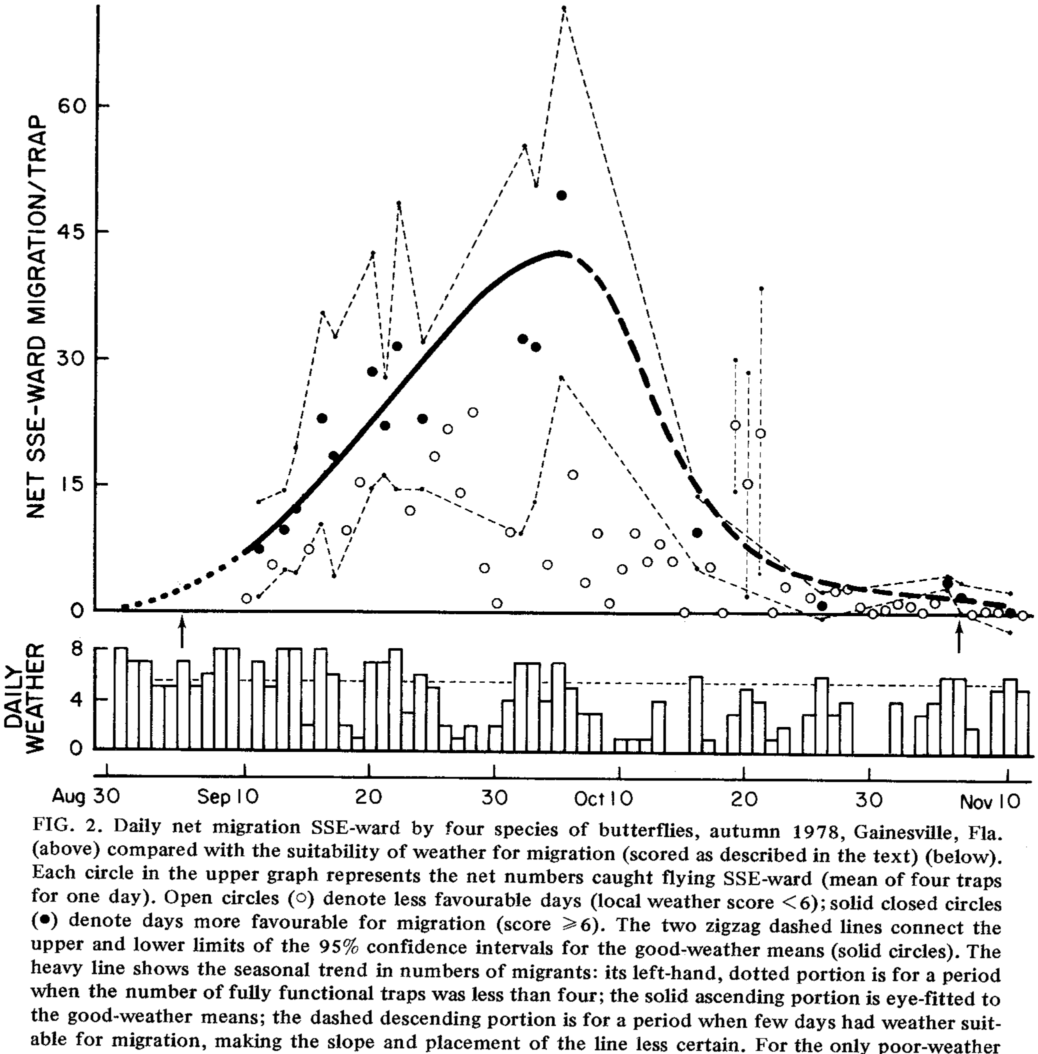

FIG. 2. Daily net migration SSE-ward by four species of butterflies, autumn 1978, Gainesville, Fla. (above) compared with the suitability of weather for migration (scored as described in the text) (below). Each circle in the upper graph represents the net numbers caught flying SSE-ward (mean of four traps for one day). Open circles (○) denote less favourable days (local weather score <6); solid closed circles (●) denote days more favourable for migration (score ≥ 6). The two zigzag dashed lines connect the upper and lower limits of the 95% confidence intervals for the good-weather means (solid circles). The heavy line shows the seasonal trend in numbers of migrants: its left-hand, dotted portion is for a period when the number of fully functional traps was less than four; the solid ascending portion is eye-fitted to the good-weather means; the dashed descending portion is for a period when few days had weather suitable for migration, making the slope and placement of the line less certain. For the only poor-weather means falling above the trend line (19, 20, 21 October), the 95% confidence intervals are shown. The period of significantly biased SSE-ward flights was 5 September to 6 November – indicated by arrows beneath the abscissa.

Days of scant migration during September and early October were invariably associated with windy, cloudy or cold local conditions.

The particular values of wind, temperature and cloud cover assumed to curtail migration were estimated from long-term but non-systematic observations and from days during this study having no migration. The original estimates were not subsequently altered to improve the fit of partially suitable days with the migration intensities of those days, but the number of favourable hours required for a good weather day (Fig. 2) was increased by one for a better subjective fit.

If only favourable days are used to establish a trend, there is a steady increase in the numbers of migrants from 11 September to 5 October. The trend after 5 October is uncertain because weather was rarely favourable. The numbers of migrants on unfavourable days (Fig. 2, open circles) are uniformly below the trend based on favourable days except for the catches of 19, 20 and 21 October. However, the 'trend' in that part of October is based on a single favourable day (16 October).

This analysis assumes that individuals trapped at Gainesville originated several hundred kilometres or more to the north. If they were predominantly of local origin, the fact that local weather explained fluctuations in their numbers would be irrelevant to Johnson's hypothesis. Their distant origin is supported by these circumstances: we know of no near-by source for millions of butterflies. Individuals of the migrating species are apparently unable to overwinter in the North (Walker 1978), but 5–10 days flight of the sort observed locally would place the butterflies in more hospitable areas 400–800 km to the south. For the most conspicuous species, *P.sennae,* flights toward Florida are seen far to the north in late summer; the dates, distances and directions are appropriate for their arriving in Florida during mid to late September (Walker, 1980).

The fact that the 10 September to 5 October trend line fits within the envelope constructed by connecting corresponding extremes of the 95% confidence intervals for days with favourable local weather (Fig. 2) suggests that numbers of migrants were gradually increasing rather than being pumped by synoptic-scale weather systems to the north. Since unfavourable local weather surely reduces the daily catch, the only variations in catch still to be explained by wind fields are deviations from the trend on favourable days and the above-trend deviations on unfavourable days (Table 1).

One might expect days with numbers above the seasonal trend to have northerly winds and days with numbers below the seasonal trend to be associated with southerly winds. In fact, on most days the 10 m wind at Gainesville (NOAA, 1978a) was from the east north-east, and if anything, above-trend catches were associated with large easterly components and below-trend catches with more northerly components (Fig. 3). The latter is likely to be the result of migrants with a tailwind flying higher within the boundary layer, thereby lessening their chances of being captured.

We addressed the critical question of the effect of large-scale wind fields on the numbers of migrants caught in the flight traps in the following manner. The net movement of a butterfly ending at the flight trap is a vectorial sum of the individual flight motion of the insect plus the environmental wind along the entire flight path. At one extreme, the insect could determine its net movement by remaining within the boundary layer where the net wind vector would be small as compared with the insect flight. At the other extreme, the

TABLE 1. Deviations from seasonal trend (Fig. 2) in daily numbers of trapped migrants. Days having unfavourable weather combined with catches less than the trend are excluded, since they call for no further explanation.

Date	No. trapped	Seasonal trend for catch during favourable weather*	Difference
Catch less than trend – favourable days			
13 September	38	44	–6
21	88	96	–8
24	96	100	–24
2 October	129	165	–36
3	127	168	–41
Catch greater than trend – favourable days			
16 September	93	64	29
17	75	69	6
20	114	92	22
22	126	104	22
5 October	202	172	30
Catch greater than trend – less favourable days			
19 October	91	38	53
20	63	31	32
21	97	28	69

* These figures may be divided by 4 to give no./trap/day (as in ordinate of Fig. 2).

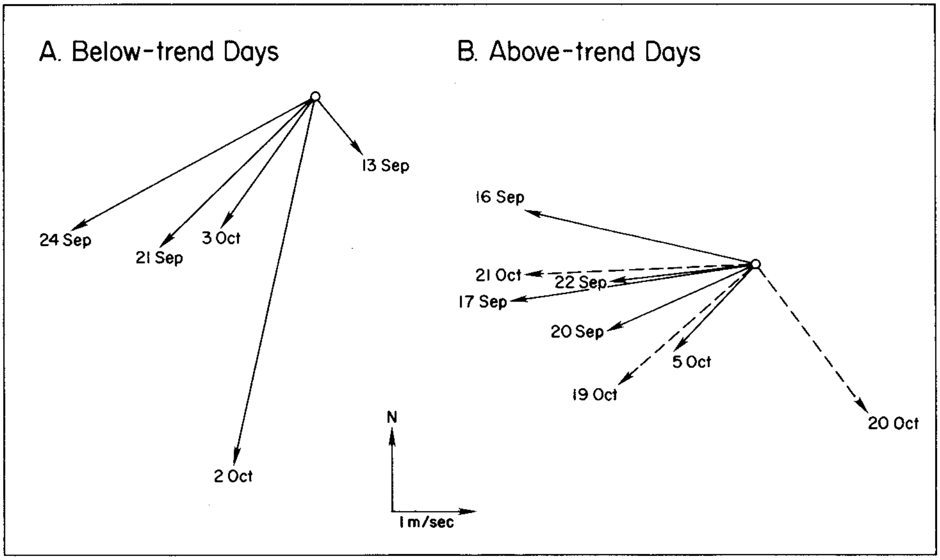

FIG. 3. Resultant winds at 10 m for Gainesville FAA Station, for the period 07.00–19.00 hours LST. **(A) Days with net SSE migration less than seasonal trend. (B) Days with net SSE migration greater than seasonal trend. (Continuous lines = favourable local weather; dashed lines = less favourable local weather; see Table 1 and Fig. 2).**

wind could determine the insect movement if random flight were sustained near tree-top level or higher. In the latter case, the insect trajectory would be indentical with the air trajectory. Air trajectories were reconstructed for all days listed in Table 1. Obtained from hourly wind observations at Gainesville, Jacksonville International Airport, Jacksonville-Craig Field, Daytona Beach, and Tallahassee (NOAA, 1978a), the trajectories describe the motion of a hypothetical air parcel at 10 m beginning somewhere upwind of Gainesville at 07.00 hours LST and ending at the flight traps at 19.00 hours LST. Although these paths strictly trace only those air parcels passing over the flight traps at 19.00 hours LST, they can be considered to represent the general wind field over north Florida. Results are illustrated in Fig. 4.

Starting locations range from about 40 km north-west to over 120 km east of Gainesville. Significantly, no obvious systematic differences in origins or routes of trajectories distinguish days with high or low catches. In ten cases the trajectories are directed predominantly southward, but in five out of the ten, catches were below the seasonal trend. The air motion is predominantly westward at 3–4 m s^{-1} for the remaining three cases, all associated with large catches of migrants.

For most of the days sampled the winds were not directed SSE along the Florida peninsula but blew across the peninsula toward the Gulf, and did not favour southward migration. In fact, the cross wind, especially prevalent in the afternoon hours, is a climatological feature of the low-level winds over north Florida in September when winds from NE to SE are more than twice as frequent as winds from WNW to NNE (ESSA, 1968).

Weather data along trajectory routes is sketchy due to the low density of surface reporting stations. However, precipitation was observed at reporting stations near trajectories on 24 September (Fig. 4, below-trend day) and 19 October (above-trend day). Weather enroute does not appear to have been an inhibiting factor accounting for the below-trend catches on 13, 21 September and 2, 3 October.

As Johnson hypothesizes, it is possible that migrating butterflies are not confined to near tree-top level during flight, but fly at higher altitudes by flying upward or being transported upward by turbulent eddies. During the day, turbulence induced mechanically and by surface heating normally maintains a well-mixed layer in the lower atmosphere which readily facilitates vertical transport.

The depth of the mixed layer over north

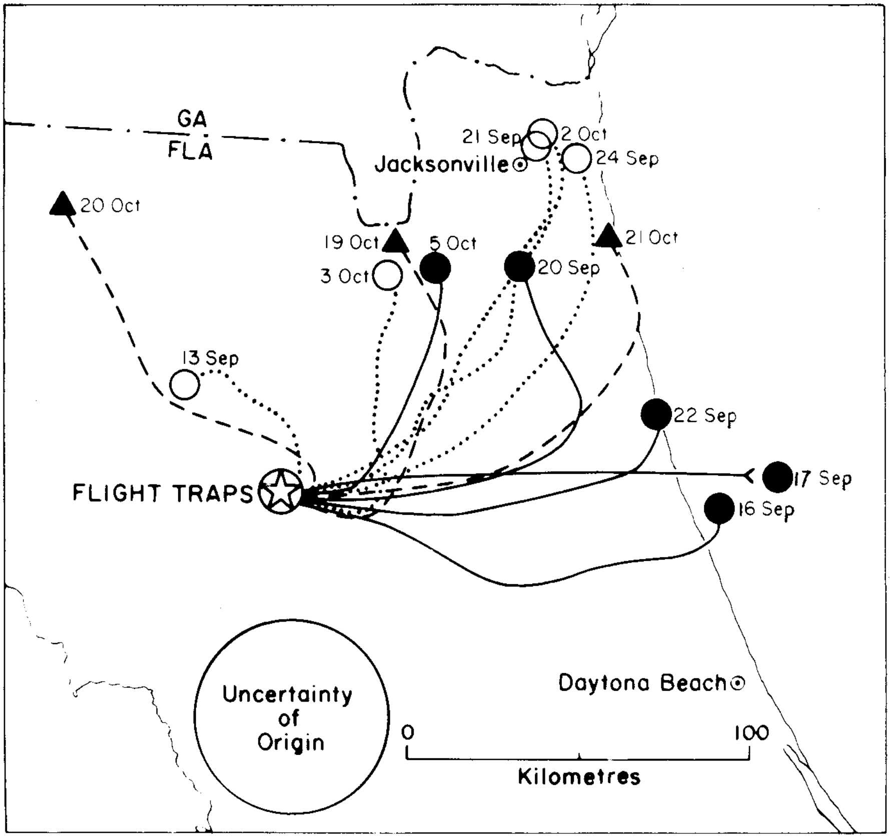

FIG. 4. Air trajectories at 10 m beginning at 07.00 hours LST and ending at 19.00 hours LST at flight traps (star) near Gainesville, Florida. Circles and triangles represent starting points, and lines represent 12 h paths for hypothetical air parcels. Open circles and dotted lines are for favourable days when net SSE migration was less than the seasonal trend. Solid circles and solid lines are for favourable days when the migration was greater than the seasonal trend. Solid triangles and dashed lines are for less favourable days having net SSE migration in excess of the seasonal trend. Dates are by each starting point. Large circle in lower right shows estimated 90% confidence limits for the mapped starting points.

Florida during the afternoon was estimated from atmospheric soundings at Waycross, Georgia, at 19.00 hours LST (NOAA, 1978b). An objective method (Heffter, 1980) yielded mixed layer depths averaging 1950 m on the days in the study sample. Trajectories based on winds near 1500 m, near the top of the mixed layer, were then constructed from twice-daily data (NOAA, 1978c). Results resemble those of Fig. 4 in that there is little to distinguish trajectories associated with above-trend numbers of migrants trapped at Gainesville from those associated with below-trend numbers.

Discussion

Neither local winds nor synoptic-scale wind trajectories accounted for variations in numbers of the four species of butterflies trapped moving southward during favourable weather. Rather, local weather conditions controlled much of the day-to-day variation in numbers. These observations indicate that the butterflies fly southward during favourable weather regardless of the favourability of the wind. If the insects' SSE direction at the flight traps is representative of their average motion along their flight path, Johnson's hypothesis is not supported. It is conceivable that the insects retain a southward flight orientation above their boundary layer while being carried generally westward or south-westward by the wind, then return to their boundary layer and are caught in the flight traps. However, it is not ecologically advantageous for the insects to make major use of winds which in a few days would carry them into the Gulf of Mexico.

Whether other butterflies migrate above their boundary layers is less certain – reports of migrating butterflies at high altitudes never include needed data on airspeed and wind, though there is generally agreement that migration in the upper air is associated with winds in the migratory direction (i.e. the heading of the butterflies is in that direction, and they fly in the same direction, but near the ground, in a head wind). The most detailed data are for the monarch and their analysis is instructive. With a tailwind, flying at heights of 2–15 m, monarchs achieved estimated ground speeds of more than 50 km h^{-1} (Gibo & Pallett, 1979). Since cruising air speed during migration is approximately 18 km h^{-1} (Urquhart, 1960), wind speed probably exceeded 32 km h^{-1}. However, monarchs flying vigorously have been said to attain air speeds of at least 40 km h^{-1} (Urquhart, 1960). Consequently, the monarchs' top air speed may have been greater than wind speeds – putting them within their boundary layer.

Whatever proves the case about use of strong winds as fast transport in a predetermined direction, there are no data, for any butterfly, supporting the hypothesis that upper air or synoptic-scale wind systems regularly determine its direction of migration. In fact, as pointed out by Baker (1978, p. 472), uncontrolled, unconditional surrender to displacement by wind 'has not yet been demonstrated for any animal.'

Acknowledgments

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